

# The Dynamics of the Lek System and Mating Success in Males of the Mediterranean Fruit Fly, *Ceratitis capitata* (Wiedemann)<sup>1</sup>

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## ABSTRACT

Experiments were conducted to investigate the dynamics of the lek mating system in the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann). The results indicate that only a portion of the total male population participates in the lek system and that among these lekking males there is differential mating success. Lekking males exhibit preference for certain territories within the lek by battling among themselves for territorial control. Females, on the other hand, appear to utilize two "lek-entering" strategies: 1) females may cue into preferred territories within the lek using a male's occupancy of such a site as an indication of his genetic fitness and 2) females may enter the lek by randomly alighting on territories and sampling the courtships of several males before selecting a mate.

The field of insect territoriality covers a broad range of phenomena intimately associated with the species' biology. Included within this array of territorial behaviors, ranging from swarm formation to solitary displays, is the lek mating system (Baker, 1983). This system involves the formation of a "lek", which is utilized as the primary courtship site for mating. Originally used only in ornithological studies, the word lek is now used in a wide range of organisms to define an aggregation of territories that is used by males for the sole purpose of mating (Wilson, 1975). A "territory" within the lek is defined as an area (e.g., a branch, a volume of air, or leaf) that is acquired and defended by a male for courtship and mating.

In the past, literature on the lek mating system had been included under the general heading of territoriality. However, in recent years, behaviorists have become more aware about this particular type of mating system primarily through information from studies of bird species (e.g., Wiley 1973, Lill 1974, LeCroy 1981). In addition, "birdlike" leks and lek behavior have been observed in a variety of other animals including the wildebeest (Wilson, 1975), two species of fruit eating bats (Bradbury 1975, Booth 1960) and endemic Hawaiian Drosophilidae (Spieth 1968). In all of these animals, the influence of the lek mating system in regulating the "effective" reproductive population warrants the study of this system as an important and separate aspect of territoriality.

Previous research on lek species has indicated that there is unequal mating success among those males that compose the lek as in manakins (Snow and Goodwin 1974) and in birds of paradise (LeCroy et al. 1980). Bradbury and Gibson (1983) discussed two possible mechanisms that could account for such unequal mating success among males of these lek species. The first possibility is that females may actively choose males in a lek. In this case, certain males must have characteristics that differentiate them from other males and which females recognize during mate selection. The second possibility is that interactions among males prior to the arrival of a female into the lek may affect mate choice. In this case, males establish a

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dominance hierarchy among themselves within the lek which, according to Bradbury and Gibson (1983), minimizes female choice.

Supporting evidence for the operation of these mechanisms has been limited; and, up until recently, lek behavior was only recorded in species of birds. Only in more recent years has the lek phenomenon been observed in other animals, and it is clear that additional detailed descriptive studies are still needed before the role of the lek system to mating success can be fully understood.

The first references on the mating behavior of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) provided basic qualitative descriptions but failed to identify the existence of lek behavior in this species (Martelli 1910, Back and Pemberton 1918, Feron 1962). Prokopy and Hendrichs (1979) were the first to recognize the lek system in the Mediterranean fruit fly with their studies of released flies in a field-caged coffee tree. Subsequent studies by Arita and Kaneshiro (in prep.) provide further descriptions of the lek system in this species as well as additional information on the environmental parameters that affect lek formation and territory selection. This study was undertaken to investigate further the role of the lek system in the mating process of *C. capitata*.

## MATERIALS AND METHODS

This study was divided into 3 experiments, each addressing a particular aspect of the mechanics of the lek system in *C. capitata*. The 1st experiment was conducted to determine what portion of the *C. capitata* male population participated in the lek and whether there was unequal mating success among those males. The 2nd experiment was conducted to investigate the relationship between preference for a territory within the lek and mating success. The 3rd experiment was conducted to investigate the relationship between territorial dominance and mating success.

The flies used in all experiments were reared from Jerusalem cherries, *Solanum pseudocapsicum* L. collected in Kipuka Ki within Hawaii Volcanoes National Park, Hawaii. Upon eclosion, flies were sexed and maintained in separate containers for at least 7 days prior to experimental use (Arita 1982). In order to assure accurate identification of the males, each male used in the experiments was color-coded by chilling at 0° C for a few minutes and then placing a spot of "Testor's" enamel on their thorax.

*Experiment 1.* Three males were placed into a glass cage (23 × 23 × 23 cm), which was provided with adult media (honey, sugar, and protein hydrolysate mixture), water, and a potted *Syngonium* plant. Males were allowed at least 24h to acclimate to the cage conditions prior to experimental use. The following morning, a virgin female was placed into the cage and her activities relative to the males in the cage were monitored. At 1500h HST the female was removed and if she had mated during the day, the color code of her mate choice was recorded. This protocol was repeated daily until 3 matings were recorded from each cage. The time interval of 0800 – 1500h HST was previously determined to be the period during which most matings occurred (Arita 1982).

After 3 matings were recorded from the cage, males were separated and placed into individual cages each supplied with adult media, water, and a potted *Syngonium* plant. Males were allowed at least a 24h acclimation period before a virgin female was placed into each of the 3 cages at 0800h. The activities of the 3 females (one female in each cage) were monitored and any matings throughout the day were recorded. The 3 females were removed at 1500h that afternoon. The next morning, at 0800h each female was placed into one of the other 2 remaining cages which

contained the males she had not yet seen. The activities of the female (relative to the males in each of the 3 cages) were again monitored and at 1500h, each female was removed. On the 3rd morning, each female was rotated and placed into the cage with the 3rd male she had not yet seen. The same observational period was used and any matings that occurred were recorded. Any female that mated during the 3-day period was replaced with a new virgin female in the transfer into the subsequent cage. Twenty-four replicates were made.

*Experiment II.* Three males were placed into a glass cage provided with adult media, water, and a potted *Syngonium* plant. Males were allowed at least a 24h acclimation period prior to experimental use. The following morning, encounters between the 3 males in the cage were recorded from 0800 – 1500 h. These observations were made for 2 more consecutive days during which time, the number of encounters, and the leaf on which each encounter occurred, were recorded.

Following the three day monitoring of male activity, males were again observed from 0800 – 1000h. Any encounters that occurred during this period were recorded. At 1000h, a virgin female was placed into the cage with the trio of males and the activities of the female (relative to the courtships of the males) were recorded until a mating occurred or until the end of the observational period (1500h). This procedure was followed until 3 matings were recorded from the cage. A total of 6 cages were observed.

*Experiment III.* Three males were placed into a glass cage supplied with adult media, water, and a potted *Syngonium* plant and allowed at least 24h to acclimate to the cage prior to experimental use. The following morning, the activities among the males in the cage were recorded from 0800 – 1000h. The number of encounters, the males involved in each encounter, and the leaf on which the encounter occurred were recorded. At 1000h, a virgin female was placed into the cage and her activity was monitored and recorded including the color code of her mate choice. At 1500h, the female was removed from the cage. This procedure was repeated for 3 consecutive days with 5 sets of cages.

The win/tie/loss record for the encounters of each male with the other males in the cage was used to calculate a dominance value. A daily dominance value (DV) for each male was calculated using the following formula:

$$DV = (\# \text{ wins} \times 0.75) + (\# \text{ ties} \times 0.50) + (\# \text{ losses} \times 0.25)$$

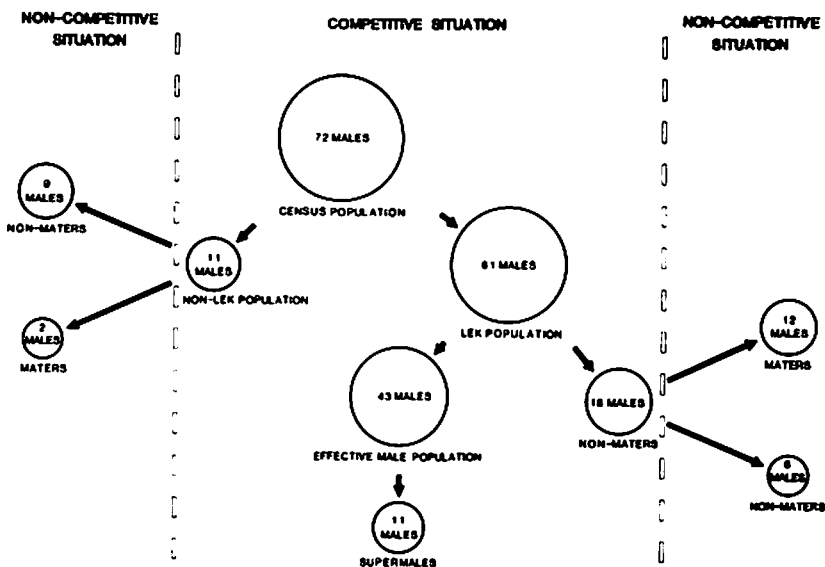
This particular weighting system gave credit to a male who continually challenged other males for territorial control but who consistently lost the battle and differentiated him from a male who never engaged in battle.

## RESULTS AND DISCUSSION

*Experiment I.* The results of Experiment I are summarized in Fig. 1. A total of 72 males were observed during this experiment. These males constituted the male "census population". From this census population, 84.7% or 61 males acquired and defended territories during the experimental period. These 61 males constituted the "lek population" and utilized the leaves of the potted *Syngonium* plants in the cages as territories.

The 11 males (15.3% of the census population) that did not acquire territories during the experimental period did not mate during the competitive phase. For the most part, these males remained on the top or bottom of the cages, and, even when females were added, these males showed very little interest in courting the females.

Not all of the males that were part of the lek population were successful in mating. Of the 61 males that constituted the lek population, only 43 males mated



**FIGURE 1.** Lek dynamics in *C. capitata* males indicating the number of males that were able to secure territories and mate under competitive and non-competitive conditions.

with the 72 females. These males formed the "effective male population". Effective in the sense that from the male census population, only 59.7% of the males were actually reproductively successful.

From the effective population, 11 males achieved 3× as many matings as the other males and were referred to as "supermales". These supermales constituted 15.3% of the male census population and were responsible for 45.8% of the matings.

After the initial experimental phase with the 3 males in each cage, the males were separated into individual cages. All males fell into two basic groups: 1) males that had mated and 2) males that had not mated while in trios. Of particular interest were the males that had not mated while in competition with other males. These males could be further subdivided into 2 groups: I) males that were part of the census population but did not acquire territories (11) and II) males that were part of the lek population (18).

In the 2nd phase of the experiment, the trio of males was separated into individual cages so that each male was not in competition with the other males. Even under these non-competitive conditions, only 2 of the 11 non-lek population males courted and mated with females. Out of 18 males that formed part of the lek population but were unsuccessful in mating, 12 of them did mate under non-competitive conditions.

The fact that 15% of the census population of males did not participate in lek formation warrants further discussion. Of significance is the availability of adequate numbers of leaves on the *Syngonium* plant that could have served as territories for all the males. Nevertheless, not all males even attempted to acquire territories. Does this mean that these non-lekking males would never become part of the lek under natural field conditions? Bradbury and Gibson (1983) proposed alternate strategies that may exist for males that are excluded from the lek but are still able to participate in mating. Prokopy and Hendrichs (1979) indicated that they observed a small percentage of *C. capitata* males waiting for females to approach host fruit (to

oviposit) and forcibly mate with these females under the semi-natural conditions of a field-caged coffee tree. Arita and Kaneshiro (unpubl. obser.) did not observe such sexual activity by males on host fruits in the natural population though laboratory reared males have been observed to exhibit such behavior. On the other hand, there were 2 males from the non-lek population that were successful in mating when separated into individual cages, which indicate that these males were just not able to acquire territories when in competition with other males. Only when these males were placed into separate cages, did they attempt to acquire a territory and, in the absence of competition from the 2 other males, mate with the female that was introduced into the cage.

The results also showed that when the lek population was presented with females, 18 out of 61 males were not successful in mating. However, when these 18 males were given an opportunity to mate under non-competitive conditions, 12 of them were able to secure mates. Thus, some of the males that were able to become part of the lek but did not mate under competitive conditions were still capable of mating.

These results indicate that while being part of the lek population appeared to be a prerequisite to mating success, it does not *assure* mating success. The males that participated in mating were from the lek population. In this population there appeared to be an elite group of supermales that achieved a larger percentage of the matings. Previous studies in other lek species, for example the sage grouse (Wiley 1973) and the kob (Buechner and Roth 1974), indicated that one male in the center of the lek was responsible for 50–70% of all copulations and that his immediate neighbors accounted for most of the remainder of the copulations. What qualities of these supermales account for their prolific mating success? In other lek species as indicated above, the qualities of the territories within the lek were not equal. There were territories that were preferred by females, and it is the male that can best defend such a territory that will be successful in copulating with the majority of the females (Wiley 1973, Lill 1974). A male can therefore increase his chances of mating in such a system if he were the occupant of a female-preferred territory.

This experiment established that: 1) not all males participated in the lek system and possibly some alternate strategy exists for some of these males; 2) being part of the lek is important in terms of mating success but does not necessarily guarantee success; and 3) there is unequal mating success among those males that do mate.

The question that still remains unanswered is whether male activity before the female's arrival at the lek or whether female choice accounts for the unequal mating success among males. Experiments II and III were conducted to investigate this question.

*Experiment II.* The results of Experiment II are presented in Table I. Although only 6 replicates were completed, the data suggest trends relevant to the dynamics of the lek system in *C. capitata*.

The data indicated that certain leaves were preferred by males as territories. Such preference for a particular leaf was determined by the number of male-male encounters that occurred on each leaf of the *Syngonium* plant. In most cases, less than 50% of the leaves served as territories on which encounters took place and on 9 of the 16 days of observation, only one leaf served as the site for most of the encounters. Yet, preference for a certain leaf on a particular day did not necessarily mean that it would serve as a preferred site on subsequent days. In 5 of the 6 cages, the preferred leaf changed from day to day. One possible explanation for the shift in the preferred leaf(s) could have been the amount of sunlight that penetrated through

the laboratory windows. Arita and Kaneshiro (in prep.) show that light plays an important role in lek formation and territorial choice.

**TABLE I.** The number of male-male encounters that occurred on each leaf and the leaf used by the female to arrive on and mate. A-G refer to the leaves of the *Syngonium* plant in the cage.

Cage #	Day	# of male-male encounters on leaf							leaf female	
		A	B	C	D	E	F	G	arrives	mates
1	1	2	0	11	0	0	0	0	A	(1)* A
	2	0	0	7	0	0	0	0	A	(1) A
	3	1	0	5	0	0	0	0	A	(3) A
2	1	5	0	0	0	0	0	0	A	(2) A
	2	3	2	0	0	2	2	0	A	(2) A
	3	1	0	4	1	0	0	0	C	(2) A
3	1	8	0	0	1	0	0	0	C	(2) A
	2	1	0	0	1	0	0	0	D	(5) A
	3	1	0	3	1	0	0	0	C	(6) A
4	1	0	3	1	2	0	0	0	A	(3) A
	2	3	2	1	0	0	0	0	A	(5) B
	3	-	-	-	-	-	-	-	-	-
5	1	2	1	0	1	0	0	0	A	(12) D
	2	0	5	0	0	0	0	0	B	(2) A
	3	-	-	-	-	-	-	-	-	-
6	1	2	3	0	0	0	0	0	B	(1) B
	2	3	12	0	0	1	4	0	B	(1) B
	3	1	3	6	0	0	0	0	B	(1) B

\*refers to the number of courtships of the female before copulation.

The results of the initial phase of Experiment II established that certain leaves were preferentially selected as territories by the males. The second phase of Experiment II was conducted to determine whether females cued into these male-preferred territories. On 9 of the 16 days, females did indeed arrive directly on the leaf that was the site of the most male-male encounters but in only 5 cases did the female mate on that site. On the remaining 7 days, the females did not arrive on the preferred territories and in fact, some of the arrivals and matings occurred on leaves that were only rarely used as territories by the males.

One of the more striking examples of a leaf that was the site of the most male-male encounters but was not preferred by females for arrival and mating occurred in Cage #1 (see Table I). On each of the 3 days of observation, leaf (C) was the site at which most of the male-male encounters took place, but all three females cued into leaf A. It appeared that, in this particular cage, the male-preferred leaf and the female-preferred site were not the same. Possibly the laboratory conditions may have somehow separated male and female preference for a site or perhaps females

were utilizing another strategy to select a mate. These results suggest the possibility that two lek entering strategies may be operating in the female population (barring laboratory effects). First, "male preferred" territories may also be preferred by females that cue directly towards these sites upon entrance into the lek since on 9 of the 16 days females did arrive on the leaf that had been the site of many male-male encounters. Thus, the male that has the ability to hold onto one of these territories would have the best opportunity to court females that arrived on such a preferred site. However, the female still has the option of leaving the territory following her assessment of the courtship display of the male occupying the preferred site. Gould (1982) suggested that the basis for the existence of this strategy is that a male's ability to gain and hold a prized territory is presumably a clue to his genetic fitness and that females have the ability to recognize such a territory. Along the same line of thought, Lill (1974) presented the concept of transferalism, in which females utilize the male's ability to secure a territory as an indication of his superior genetic fitness in the same manner as she would utilize a male's courtship repertoire. Lill indicated that the use of preferred territories in the lek system of certain animals helps to explain why these territories are so highly sought and battled for by males.

In the second strategy, "male-preferred" territories may not necessarily be the site of the arrival of the female into the lek. Instead females appear to sample the courtships of males randomly as the primary means of selecting a mate. The assessment of a male's ability in performing courtship signals has been recognized as a major determinant in mate choice in animal species even among lekking species (Spieth 1974).

Wiley (1973) indicated that both strategies may be present in the sage grouse. He observed that during the early part of the breeding season, females cue toward preferred territories while during the later part of the season, females appear to sample the courtships of males as the primary means of mate selection.

Gould (1982) discussed the adaptive significance of evolutionarily stable strategies that may be applicable in this situation. He stated that "... external events serve simply to shift the balance among a preordained set of behavioral responses available to the organism. Initially, this view seems at odds with our notions of instinct and the optimum programming we have come to expect from our genes. Surely one unique best solution exists. But if we think about it, behavioral variability and even unpredictability may have its advantages . . ."

*Experiment III.* The results of Experiment III are presented in Table II. On several days, the number of male-male encounters were few, and on such days a dominance value for each male was not calculated because these values would not have been an accurate representation of male activity in the cage.

The results indicated that in most of the cages the same male did not remain dominant for all 3 days. In fact, in 2 of the cages, the most dominant male on one day was the least dominant on another day. These changes in dominance hierarchy may be a reflection of the dynamics of the lek system as males jockey for control of a preferred site.

Once the preferred site and dominance hierarchy had been established, the relationship between dominance and mating success was investigated in the 2nd portion of the experiment. The results of this phase of the experiment are also presented in Table II. These results must be assessed in view of a particular behavior of lekking males. Usually a male will defend his territory against all intruders. Occasionally, a male who occupies a preferred territory was observed to leave his territory, move to another territory, or simply fly around the cage then return to his

**TABLE II.** Dominance values for *C. capitata* males on days when the female arrived on the leaf with the most male-male encounters (i.e., preferred territory) and the male that mated with the female.

Cage #	Day	Dominance Value (DV)			Successful male
		Red male	Blue male	Yellow male	
1	1	1.75	3.25	-	red
1	2	0.75	5.49	0.22	red
1	3	1.50	0.42	3.00	yellow
3	3	2.00	0.42	1.80	yellow
4	2	2.00	2.01	2.24	blue
5	1	2.25	1.50	0.75	red
5	2	9.24	6.05	4.80	red

original territory. During his short departure from a preferred site, another male, usually the male who has been challenging the resident for territorial control will move onto the temporarily vacated site. Upon his return, the dominant male will usually regain control of his territory. Should a female cue into the preferred site when it is temporarily occupied by a "transient" male, this male will have the first opportunity to court the female.

Of the 13 days when a dominance value could be assessed to each male, only on 7 of those days did females cue into the preferred territory. On 3 of the 7 days, the female mated with the male that had the highest dominance value which was substantially higher than the dominance values of the other males in the cage. On 2 of the remaining 4 days, the dominance value of the male that mated, though not the highest value, was not significantly lower than the value of the dominant male. On the remaining 2 days, the female mated with the male with a considerably lower dominance value but in these 2 cases, these males were occupying the temporarily vacated preferred territory when the female arrived.

The following trends appear to operate when females cue into preferred territories. The determination of the preferred territory appears to be at least in part influenced by the amount of light filtering into the cage and through the leaves of the plant. Each day, males in the cage jockey for possession of the preferred territory. The male that is successful in occupying the preferred territory when a female (utilizing the lek-entering strategy of cueing into a preferred site) arrives will have the first opportunity to court the female. The dominance values as calculated through the win/tie/loss record of a male's encounters with the other males in the cage can be used as an indicator of mating success when one male has firmly established his dominance over the other males in the cage. Only in cases where the dominant male of a preferred site temporarily vacates his territory or when dominance is not firmly established will the lesser males in the cage have the first mating opportunities with females that cue into a preferred site.

The 6 females that did not cue into preferred territories in their respective cages appear to "sample" the courtship displays of all 3 males randomly before selecting the male with which she will mate. Indeed, these kinds of females may also mate with males that occupy preferred territories but the difference here is that these females allow less dominant males the first opportunity to court. It would appear



then, that this second lek-entering strategy may be an important part of the mating system in this species in order to maintain a range of mating types in the population. Clearly, further studies are necessary in order to confirm these notions.

### CONCLUSIONS

The results of the experiment clearly indicate that the lek system in *C. capitata* affects the number of males that participate in reproduction. Only a portion of the total male population compose the lek. Of these males, only a smaller portion will be reproductively successful.

The ultimate question of what role the lek system serves in mate choice once a female enters the lek is still far from being answered. Insights from this study suggest that two lek-entering strategies may be employed by females. One strategy is based solely on female choice through courtship encounters with several lekking males. In this case, the lek only serves to attract females to a localized assembly of males. Once at the lek, the female relies on the courtship repertoire of the males in her mate selection process. In the second strategy, females may actively seek out the male who occupies a preferred territory. In some cases a male's dominance of a preferred site can be equated with mating success.

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